

UPLAND BOREAL FOREST SUCCESSIONAL PATHWAYS NEAR FAIRBANKS,

ALASKA

By

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QUANTIFYING UPLAND BOREAL FOREST SUCCESSIONAL PATHWAYS NEAR  
FAIRBANKS, ALASKA

A  
THESIS

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## ABSTRACT

Previous studies have suggested that post-fire forest succession in Interior Alaska can occur in two different ways. Self-replacement occurs when pre-fire dominant species immediately replace themselves as the canopy dominants after fire. Species-dominance relay occurs when, after simultaneously establishing themselves after fire, deciduous trees relinquish canopy dominance to conifer species as the stand ages. The relative importance of these different successional processes at landscape scales in Interior Alaska is unknown. To test for the importance of these two trajectories, we built a multinomial logistic regression model explaining the relationship between classified vegetation type and topographic variables. We also determined the relative occurrence of species-dominance relay by comparing aged stands to known successional patterns. The model correctly predicted 78% of spruce distribution, and the majority of stands are not following the species-dominance relay pattern, implying that most of the study area appears to be following a self-replacement trajectory with only a small proportion of sites capable of supporting both deciduous and spruce species. These results have important implications for modeling forest succession in Interior Alaska because of the importance of these dynamics in determining the fire regime, carbon storage, and global warming scenarios.

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## Introduction

The forest of Interior Alaska, the region between the Alaska and Brooks Ranges, is a mosaic of stands varying in age and species composition. What factors control this mosaic? Two hypotheses immediately suggest themselves. First, the mosaic may be the product of a single, widespread successional sequence interacting with burn scars of different ages. Different parts of the boreal forest landscape have burned at various times in the past, so different stages of the same general sequence of vegetation succession occur on different parts of the landscape (Van Cleve et al. 1991). The alternate hypothesis is that the boreal forest mosaic is a product of microclimatic variability across the landscape. The arrangement of the mosaic is more or less unchanging because different sites on the landscape experience different microclimatic regimes that affect vegetation distribution. Alternatively, and most likely, the vegetation mosaic we see in the boreal forest is the outcome of the combined effects of both time-since-last-fire and microclimatic variability.

Secondary succession in Interior Alaska has been driven by fire for tens of thousands of years (Lynch and Clark 2003). Fire and vegetation dynamics are constantly interacting through positive and negative feedbacks and through spatial and temporal patterns depending upon several factors including topography, weather, and vegetation composition and distribution. Fire intensity and resulting severity is generally greatest in black spruce stands (Bonan and Shugart 1989), but are often dependent on stand density

fairly well  
documented  
✓ for fire  
in PIMA, but  
disturbance  
is much  
less so

✓ state  
factors

as well (Arseneault 2001). While this pattern is common, it also depends on how the contrasting vegetation types are distributed. If large contiguous patches of similar cover types are present, this often accentuates the effects of fire (Rupp et al. 2000). This may result in complete consumption of organic matter in coniferous vegetation, or the extinguishment of fire in deciduous types. Fire frequency is also influenced by vegetation type. Coniferous vegetation has a higher probability of burning due to its growth structure, chemical makeup, and often-dense understory (Viereck 1983). Deciduous tree species are more difficult to burn because of high moisture content and a relative lack of low branches and understory fuels (Chapin et al. 2003).

✓ why fire breaks are sought - to reduce contiguity

✓ why focus on tree conversion

While interactions between fire and vegetation are often complex and not easily studied, the related pattern of vegetation and fire with topographic variables can be quantified. Topographic variables such as slope, aspect, elevation, and resulting hydrology and solar radiation patterns all affect how and where vegetation grows and fire burns across the landscape (Ryan 2002). These spatial variables are easier to study because they are constant through time relative to vegetation growth and fire regime.

Boreal tree species distribution is often limited by physiological tolerances based on topography (Bridge and Johnson 2000). These species-specific thresholds determine habitat suitability. For instance, though quaking aspen (*Populus tremuloides*) occurs within the zone of discontinuous permafrost, it is largely restricted to sites with thick



(>1m) active layers. These sites are usually found on south facing aspects with abundant solar radiation. Black spruce (*Picea mariana*) is adapted to wet organic soils, and its shallow rooting habit has allowed it to survive on permafrost sites with thin (<1m) active layers (Viereck and Johnston 1990). Because of the low sun angle in Interior Alaska, these permafrost areas are usually found on north-facing sites or in valley bottoms where very little direct solar radiation is found. White spruce (*Picea glauca*) survives on a range of sites but will not tolerate cold or waterlogged soils (Nienstaedt and Zasada 1990) that occur in valley bottoms where water pools and permafrost forms. Paper birch (*Betula papyrifera*) grows best on sites that are free of shallow permafrost but also occur occasionally on north-facing sites with deeply thawed and well-drained soils (Neiland and Viereck 1977).

These physiological tolerances limit where the different tree species are able to grow. This has significant implications for what successional pathway will be followed at a site. Previous studies suggest two general models of post-fire secondary succession that direct stand development.

Species-dominance relay (SDR) involves shifts in the dominant overstory species. (Clements 1916; Egler 1954; Drury and Nisbet 1973; Connell and Slatyer 1977). In Alaska, this model predicts initial colonization of a burned site by herbaceous vegetation, followed by the establishment of deciduous and coniferous tree species. Deciduous tree

species of paper birch and quaking aspen initially dominate the forest canopy until black or white spruce take over and maintain their dominance until the next fire (Viereck and Shandelmeier 1980; Van Cleve and Viereck 1981; Foote 1983; Yarie 1983). In SDR, time-since-last-fire is a major determinant of species dominance at a site as well as the landscape-scale mosaic of vegetation distribution.

Self-replacement (SR) is the alternate mechanism of secondary succession to SDR. It involves the immediate post-fire replacement of the pre-fire dominant species. In the case of birch and aspen, SR predominantly involves vegetative reproduction after fire, as seedling reproduction is infrequent (Zasada et al. 1992). Aspen is a vigorous root-sprouter (Lutz 1956; Barnes 1966; Safford et al. 1990; Greene et al. 1999) that quickly re-dominates a site following fire and effectively out-competes other species by extremely fast growth into the canopy. Aspen also inhibits other species from establishing because of accumulation of organic matter, which prevents other species from germinating (Carter and Chapin 2000). While not as prolific, birch is also able to vegetatively reproduce through basal sprouting and produces large quantities of light seeds that are widely disseminated following fire (Safford et al. 1990; Greene et al. 1999).

In the case of black spruce, SR involves seeds dispersed from unburned cone crops stored in the crowns of trees. The semi-serotinous cones in the upper canopy of black spruce

allow it to quickly colonize a site following fire (Viereck and Johnson 1990; Greene et al. 1999). Black spruce is able to survive on a variety of sites, but out-competes other species on cold, wet sites underlain by permafrost (Van Cleve et al. 1983) through its shallow root growth and ability to conserve nutrients (Wheeler 2004). SR strategies have been shown to occur in the boreal forest on black spruce sites (Viereck and Shandelmeier 1980; Foote 1983) as well as in deciduous communities (Mann and Plug 1999; Cumming et al. 2000; Johnstone 2005; Johnstone and Chapin 2005).

Fire is the most significant disturbance in the boreal forest. Fires burn an average of 350,000 hectares each year in Alaska. This prevalence of one disturbance agent has linked fire with vegetation and climate patterns in driving boreal ecosystems. The frequency and severity of fire in the boreal forest is highly dependent upon vegetation type, and estimates of fire frequency range from 50-200 years (Viereck and Shandelmeier 1980; Yarie 1981) for Interior Alaska. All Alaskan boreal tree species have thin bark and are commonly killed by wildfire. Stand-replacing fires are common within highly flammable black spruce stands. Other disturbances such as wind throw and insect damage occur on relatively small scales compared to fire and so do not affect vegetation patterns to the same degree.



Despite the limited number of tree species in Interior Alaska and its relatively simple fire dominated disturbance regime, the ecological processes that drive post-fire secondary succession remain poorly understood in the boreal forest. These processes are important for modeling vegetation dynamics, which has been hampered by our understanding of the relative importance of these two successional trajectories. These models have many goals such as predicting carbon dynamics (Zhuang et al. 2002) simulating warming scenarios (Shaver et al. 2000), or modeling future fire behavior (Ryan 2002). The results of these models rely heavily on how the vegetation dynamics are represented. Previous modeling efforts have identified that the relative importance of each successional trajectory in Interior Alaska is poorly understood and insufficient for modeling future fire scenarios (Rupp et al. 2002; Chapin et al. 2003). By deciphering the forest mosaic, we are quantifying the importance of the mechanisms that drive secondary succession. Understanding these mechanisms is critical for an improved understanding of boreal forest processes that will allow us to accurately model and predict future vegetation distribution, fire occurrence, and carbon allocation.

In this study, we build a statistical model relating classified vegetation types to various topographic variables. We then develop probability functions that determine what areas are able to support each species and infer the most likely successional trajectory.

Additionally, we reconstruct growth histories in two stands suspected to have followed the SDR model of succession. Finally, we compare these growth patterns to other aged

stands to see if similar patterns are followed in order to infer the relative importance of SDR and SR on a landscape scale.

## **Methods**

### ***Study Area***

The study area is a 47 km<sup>2</sup> drainage on the north side of Ester Dome (148° 7' 0.09"W, 64° 53' 1.08"N) 19 km northwest of Fairbanks, Alaska (Fig 1). Elevation ranges from 140 meters in valleys to 770 meters on ridge tops. This region of Alaska is characterized by a continental climate (Haugen 1982) with large seasonal fluctuations in temperature due to widely varying amounts of solar radiation throughout the year (Slaughter 1986). With 18-21 hours of sunlight during the summer months of June, July, and August, daily temperature highs reach the mid 20s °C with extremes above 30 °C. In contrast, winter months have only 4-10 hours of sunlight and low temperatures below - 40 °C (Alaska Climate Research 2005). A below freezing mean annual temperature allows discontinuous permafrost to form in the area. Precipitation is generally low, averaging 270 mm, most falling as rain in the late summer months. Snow cover usually persists from mid-October until mid-April (Alaska Climate Research 2005). The geology of Ester Dome consists of schists with igneous intrusions overlain with loess and gravel of varying thickness depending on slope position.

Our study area is representative of hilly terrain in the boreal forest of Interior Alaska. Sharp boundaries separate stand types along topographic breaks and at the boundaries of past disturbances. The topographic complexity results in a mosaic of contrasting thermal regimes caused by the combined effect of low sun angles and hill-slope shading. Black spruce is found on north-facing sites with cold and often frozen, moist soils; while quaking aspen and paper birch species are found on warmer south-, west-, and east-facing slopes. In our study area, white spruce is a small component of the total vegetation composition and is restricted to relatively flat ridge tops.

### *Image Classification*

We extracted response variables for use in a logistic regression model relating classified vegetation types to topographic variables. We obtained a subset of a Quickbird satellite image of our study area in order to classify the major vegetation types. The image was collected in late summer 2001 with a 60 cm spatial resolution, 16-bit radiometric resolution, and red, green, blue, and infrared spectral bands. We utilized ERDAS IMAGINE 8.6 image processing software (<http://www.gis.leica-geosystems.com/Products/Imagine/>) for the vegetation classification. A radiometric enhancement noise-reducing filter was applied to the image in order to reduce some of the pixelization in the image. This tool preserves subtle details in an image while



removing noise along edges and in flat areas. The high spatial resolution along with the low sun angle in Alaska resulted in significant shadowing between individual tree canopies, which interferes with classifying image pixels into distinct vegetation categories. A 12x12 low-pass filter was applied in order to reduce the influence of the shadows on the final vegetation classification. This technique averages together a 12x12 pixel area around each pixel in the image. Low frequency components (e.g. shadows) were passed and high-frequency components were attenuated.

We performed a supervised classification of major vegetation types in our study area using the final modified image and the maximum likelihood method. Training areas were manually delineated into 5 cover types of spruce, quaking aspen, paper birch, alder, and bare ground with 20, 14, 14, 19, and 20 training areas, respectively. Training areas were located across the entire study area in order to capture the entire range of spectral signatures for each cover type.

Normally, aspen and birch cover types would not be easily distinguished from each other on satellite imagery due to similar growth structure and reflectance characteristics. In our case, the image was captured during a significant infestation of aspen leaf miner (*Phyllocnistis populiella*) insects that prefers aspen as its host. The larval stage of this insect mines the leaf tissue, which decreases chlorophyll content and alters the

reflectance of aspen foliage enough to allow both visual and spectral separation between aspen and birch cover types (Strailey 2004).

Field verification was completed on 53 randomly distributed points across the entire study area. We used a Trimble GeoExplorer 3 GPS unit to navigate to these points and visually inspect them by determining what species had the majority of canopy coverage and site dominance. We used a 10-factor prism to determine basal area by tree species. True cover type was noted based on both a subjective total site dominance determination and an objective basal area measurement. This verification protocol was followed because the satellite image spectral response was mainly due to overstory canopy conditions and some species may have canopy dominance but not basal area dominance. This process allowed a distinct cover type to be determined for all sample points. Error matrices were developed for classes used in the supervised vegetation classification.

### ***Model Variables***

Covariate variables of elevation, slope gradient, slope aspect, and water flow were derived from a 5-meter digital elevation model (DEM). In addition, summer solar radiation was estimated from a 20-meter elevation model (Table 1).

A 20-meter spatial resolution spaceborn-derived SAR DEM was obtained. This image ✓  
 was used within the Solar Analyst extension for ArcView  
 (<http://www.fs.fed.us/informs/download.php>) to calculate total global summer insolation *use dates*  
 from May 15<sup>th</sup> until August 15<sup>th</sup> (Fu and Rich 1999). We used global insolation because ✓  
 both direct and diffuse radiation contribute to the varying site conditions that affect how  
 species grow. The time period for radiation calculations were used because they ✓  
 represented dates of approximate spring leaf-out and fall senescence for Interior Alaska *source?*  
 tree species. Insolation transmittivity, or the percent of global radiation that is diffuse, ✓  
 was calculated as 52.4 percent (Anderson et al. 1980; Wendler and Eaton 1983). We *? what does that mean?*  
 utilized the uniform sky diffuse model for diffuse radiation calculations. The Solar  
 Analyst extension generated an upward-looking hemispherical viewshed for every  
 location on the DEM. The hemispherical viewsheds were then used to calculate  
 insolation for each location accounting for site latitude, elevation, surface orientation,  
 shadows cast by surrounding topography, daily and seasonal shifts in solar angle, and  
 atmospheric attenuation. The final product was a grid of insolation estimates in total watt  
 hours/m<sup>2</sup> for the entire summer.

We obtained a 5-meter spatial resolution Airborn-derived SAR DEM to calculate the  
 remaining model covariates within ArcGIS 9.0 (ESRI, Arc/Info license). Water flow to  
 each grid cell in the DEM was determined using various hydrology tools within  
 ArcToolbox. First, minor data errors within the DEM were identified using the sink tool.



These were then filled in with the fill tool. This corrected DEM was then used within the flow direction tool to determine which of eight directions a given cell would flow toward. Finally, the flow direction grid was used within the flow accumulation tool to determine the total number of upslope cells flowing through or to each down-slope cell. Slope gradient and slope aspect were calculated using tools within the Spatial Analyst extension.

One thousand points were randomly located within the study area. Points falling in grid cells classified as bare ground were eliminated and 772 sample grid cells with vegetation class and covariate variables were exported for logistic regression modeling.

### ***Modeling***

We determined the relationship between the classified vegetation types and topographic variables and how much of the current vegetative cover could be predicted by spatial variables based on topography alone. SPSS 12.5 (<http://www.spss.com/>) was used for all model development. We used a multinomial logistic regression model (Hosmer and Lemeshow 1989, Davis and Goetz 1990; Augustine et al. 2001) with our response variable containing three levels of vegetation classes (spruce, aspen, birch). Model covariates were summer insolation, water flow, slope gradient, slope aspect, and

elevation. The logit link function was used and probabilities of class membership were  $\wedge$  derived from parameter estimates.

Potential sources of multicollinearity between variables were investigated. No automated model selection procedures were incorporated which allowed us greater control over any multicollinearity effects. A two-stage manual model selection methodology was  $\vee$  incorporated. The saturated model included all main effects and two-way interactions. At stage one, interaction terms with significance greater than 0.2 were eliminated from the model. At stage 2, any term with significance greater than 0.05 were eliminated until all terms were significant ( $\alpha = 0.05$ ). The final model was chosen based on all of the  $\wedge$  parameters being significant as well as having the highest predictive ability based on the classification table.

The final model was validated within the R 2.0.1 statistical package using the multinom function within the nnet package (<http://www.r-project.org>). A new random sample of 1000 was taken from the grids and the bare ground class deleted for a sample size of 775. The final model was run using the new validation sample as covariate inputs. Probabilities of membership in each class were calculated and a validation classification table was developed.

*bare ground class?*

### ***Stand Reconstructions***

We reconstructed age-canopy height patterns in two mixed birch/black spruce stands suspected of following the SDR model of succession. The presence of vigorous black spruce dominating the canopy along with similar numbers of senescing paper birch below the dominant canopy suggested the occurrence of SDR in these stands. This stand structure suggested that the birch had initially dominated the canopy and was now being over-topped by black spruce. Site one is east-facing and site two is southeast-facing. Both are situated at 475m elevation. We felled pairs of black spruce and paper birch growing closely adjacent to one another. Five pairs of trees were felled at Site 1 and six pairs at Site 2. Trees were cut as close to the ground as possible and height above root collar was estimated by digging down and visually inspecting the root-shoot interface. Total bole height was measured as height above root collar. Cross sections were taken at 1-2 meter intervals up the bole of the tree. In the laboratory, cross sections were smoothed with a belt sander using 220-, 400-, and 600-grain sandpaper and annual rings counted using a dissecting microscope.

### ***Stand Border Sampling***

We used Quickbird satellite imagery to identify distinct spruce and deciduous stand borders. We sampled sixteen randomly selected pairs of deciduous and coniferous stands located adjacent to one another across common borders (Fig 2). These borders comprise



approximately half of all the readily identified borders separating different stand types in the study area. The sampled borders and the stands they separate occur across all geomorphic positions: valley bottoms, ridge tops, and gradual toe slopes. This variety of landscape positions captures most of the variation in topographic and microclimate conditions within the study area.

Border coordinates were transferred from georeferenced Quickbird imagery to a Trimble GeoExplorer 3 GPS unit in order to locate them in the field. Fifteen trees were sampled along a random length transect in each paired stand within 50 meters of the border. All stands were homogeneous in tree size and canopy height with only one major age class represented. Spruce stands were largely monospecific with less than 10% deciduous species. Deciduous stands were also largely monospecific or a mixture of paper birch and quaking aspen with less than 10% spruce. When a mixed birch-aspen stand was encountered, the sampling intensity was determined by the relative dominance of each species distribution in the stand. Co-dominant trees in both bole size and height were chosen in order to obtain an accurate estimate of stand age. Obvious dominant trees that were most likely survivors of past fires, as well as young trees that may have colonized after the initial establishment period, were avoided. We cored trees using an increment borer bit in a standard 18-volt cordless drill. Cores were taken an average of 11 cm (range 4.4 – 20.2 cm) above the ground to obtain an accurate germination age while avoiding the

root mass at the base of the trees. We used a laser hypsometer to record tree height. We cored a total of 480 stems in 32 stands covering 16 stand borders.

Cores were mounted on wooden mounts with glue in the same orientation as they grew in the tree, trimmed to size, and labeled. Once dry, the cores were hand sanded using 220-, 400-, and 600-grain sandpaper and annual rings counted using a dissecting microscope.

An age correction method based on core and total tree height was not used because we determined that the resulting age corrections were insignificant and would not affect our results. ✓  
P. what is  
this?

### ***Testing the SDR Hypothesis***

Successional stand age requirements were determined from the stand reconstruction results by estimating times from stand establishment until distinct stages in succession. These stages included a co-dominance stage where both species are in the upper canopy and a spruce dominance stage where canopy dominance is relayed to spruce. These age requirements for SDR succession were then compared to the sampled border stands to see if similar patterns are followed. We purposefully underestimated the time required for SDR to occur between birch and spruce to be conservative in our conclusions.

The R 2.0.1 statistical package (<http://www.r-project.org/>) was used for all statistical tests. Our low sample size of 15 cores per stand prevented us from assuming normality or common distributional shape between samples, so all tests were completed using both parametric t-tests and non-parametric Mann-Whitney tests. T-tests assume normality and provide for unequal variances, but are influenced by outliers. Mann-Whitney tests do not assume normality and are robust to outliers, but do assume samples only differ in location (i.e. mean or median) but not in their dispersion or distributional shape. If test results conflicted, the Ansari-Bradley test of dispersion (Hollander and Wolfe 1973) was used to determine if the samples differed in scale (i.e. variance). If the Ansari-Bradley test indicated unequal dispersions, the t-test result was accepted because of its allowance for unequal variances, otherwise the Mann-Whitney result was assumed to be more accurate.

## Results

### *Image Classification*

The supervised image classification (Fig 3) was validated for classes used in the final logistic regression modeling process. The error matrix (Table 2) indicated user accuracies of 70% for alder, 57% for aspen, 92% for birch, and 100% for spruce. Producer's accuracy was 78% for alder, 67% for aspen, 92% for birch, and 92% for spruce. Overall accuracy was 87% with a kappa statistic of 81%.

*supervised image  
classification?*



### ***Modeling***

During model development, it was determined that the alder class was the most difficult to predict using the topographic covariates we chose and is not an important species in either successional pathway, and so was dropped from the analysis. The final model included aspen, birch, and spruce as response variables and insolation and elevation as significant ( $\alpha = 0.05$ ) covariates (Fig 4). The model predicted correctly 18.2% of aspen, 47.5% of birch, and 78.6% of spruce with an overall accuracy of 55.3%. The validation model predicted correctly 12.4% of aspen, 43.4% of birch, and 77.9% of spruce with an overall accuracy of 50.8%. The probabilities of class membership given insolation and elevation values are presented in Fig 5. The probability of a site being dominated by spruce is much higher than any other vegetation type and gradually declines from high elevation/low insolation sites to lower elevation/higher insolation sites. Birch is predicted to occupy a relatively small region of lower elevation warm sites, while aspen is predicted to occupy only the warmest sites, but over a wide range of elevations.

Probabilities of class membership for the spruce/aspen and spruce/birch associations were plotted to show what regions of the landscape could be simultaneously occupied by both species and so theoretically able to support a SDR successional trajectory (Fig 6). The spruce/aspen SDR trajectory occurs on warmer sites across a wide range of elevations. The spruce/birch SDR trajectory occurs over a wider insolation range but on a narrower elevation range than the spruce/aspen trajectory. Large regions of the solution surface

will most likely support only a SR trajectory because the probability of supporting both spruce and deciduous species is low (Fig 7).

### ***Stand Reconstructions***

Stand reconstruction results are presented in Fig 8. The apparent lack of growth in the second half of the total lifespan of birch is due to rotten tops breaking off, so final birch height underestimates the maximum height reached by these trees earlier in their life spans. The ranges for each successional stage were determined by interpretation of the graphical results and estimating when the birch trees began to relay canopy dominance to spruce.

Site 1 indicated paper birch might have been present on the site earlier than black spruce, although both species were present within approximately 30 years following stand initiation. Birch trees initially grew at a faster rate, dominating the canopy for approximately the first 140 years. There was a transitional co-dominance of birch and black spruce from as early as 140 years to as late as 190 years after the initial birch establishment. Spruce assumed canopy dominance as early as 150 years or as late as 170 years after spruce establishment.

Site 2 indicated both tree species established at the same time. Paper birch grew at a faster rate and dominated the canopy for approximately the first 110 years. As at Site 1, there was a transitional co-dominance of birch and black spruce from as early as 110 years to as late as 160 years after stand establishment. Spruce assumed canopy dominance as early as 130 years or as late as 180 years following establishment.

### *Tests of Successional Pathways*

As the SDR model explains, if SDR has occurred widely in the study area, adjacent stands of deciduous and spruce should differ in age, with the spruce stands being older. And based on our stand reconstruction results, the spruce stands should be greater than 100 years old, and there should be ample evidence of past dominant deciduous trees.

Four of the 16 paired stands (1, 12, 13, 14) had no significant age difference ( $\alpha = 0.05$ , Fig 9). This suggests that these pairs of stands do not represent different stages in a SDR successional trajectory, because spruce stands theoretically can never be the same age as deciduous stands under the SDR hypothesis. ✓

Nine of the 16 spruce stands (1, 4, 5, 6, 7, 9, 12, 13, 14) were significantly younger than 100 years ( $\alpha = 0.05$ , Fig 9). These stands could not have passed through deciduous stages because they lack any deciduous trees despite their young (<100 years) ages. Based on



our two stand growth reconstructions, spruce dominated stands theoretically cannot be less than 100 years old under the SDR hypothesis.

Five of the 16 spruce stands (3, 10, 11, 15, 16) were significantly older than 100 years ( $\alpha = 0.05$ , Fig 9), but there was no evidence of birch or aspen species that had dominated the site at any level in the past. The only deciduous tree species present were scattered patches of alder at spruce stands 10 and 11. Stands 3, 15, and 16 were monospecific, dominated by spruce trees. This lack of evidence of past deciduous domination does not conform to the SDR assumptions in spruce stands greater than 200 years old. Therefore, the majority of spruce stands are unlikely to have originated through SDR succession and more likely have followed a SR trajectory of succession.

## **Discussion**

### ***Modeling***

The image classification was accurate and provided a strong response variable surface to develop the multinomial logistic regression model and provide accurate results. Summer insolation and elevation covariates predicted over half of the total species current distribution. The individual spruce cover type was correctly classified 78% of the time in both the initial and validation model. SDR assumes that stand dominance will relay over time from deciduous to spruce cover types, and that time-since-last-fire is a major

determinant of stand dominance. Our ability to predict 78% of spruce distribution based solely on spatially determined variables strongly suggests that SDR is not the dominant successional trajectory in this area. If SDR was occurring across the study area, each cover type should be correctly classified at approximately the same percentage because every site would go through both deciduous and spruce stages. However, this is not the case, suggesting that SR is the dominant successional trajectory.

SR has been shown to occur in deciduous stands with a brief fire return interval and clonal abilities (Mann and Plug 1999; Cumming et al. 2000; Johnstone 2005; Johnstone and Chapin 2005) as well as in black spruce stands (Van Cleve and Viereck 1981; De Grandpre et al. 2000; Johnstone 2005) through a large viable seed crop after fires. White spruce may even self-replace if a seed source is available and site conditions optimal (Van Cleve and Viereck 1981).

The SDR response surfaces that show areas where spruce and deciduous species are able to coexist (Fig 7) give the impression that SDR is possible across the majority of the study area, but we believe it is limited to many fewer sites. First, if spruce is the canopy dominant before fire occurs, the site will likely experience SR because of the low chances of deciduous species invading before spruce seed in from readily available sources in the canopy. Second, a short fire return interval is most likely limiting SDR from occurring

because fire occurs before these possible SDR sites have time to relay dominance to spruce (Mann and Plug 1999).

### ***Stand Reconstructions***

Both of our stand reconstructions (Fig 8) revealed that both black spruce and paper birch species established within 20 years following fire. This pattern of immediate establishment by all tree species is similar to those found on white spruce/deciduous sites (Viereck and Shandelmeier 1980; Van Cleve and Viereck 1981; Foote 1983; Van Cleve and Viereck 1983) and on upland mesic black spruce/deciduous sites in Interior Alaska (Foote 1983; Van Cleve and Viereck 1983). Past studies have found that aging trees above the root collar consistently underestimates germination age in boreal species, with coniferous species being more severely underestimated (0-43 years) than deciduous species (0-11 years) (DesRochers and Gagnon 1997; Gutsell and Johnson 2002). The germination dates of black spruce in our reconstructed stands are most likely underestimated. Additionally, most of our germination dates had to be sampled from sections up the bole of the trees, as many ground level samples were too rotten to be accurately aged. For these reasons, we believe both black spruce and paper birch germinated on the sites within a few years following fire, which is consistent with past post-fire germination studies (Gutsell and Johnson 2002).



Foote (1983) found that on upland mesic black spruce sites, paper birch and aspen dominated the site for the first 50 years following fire while other researchers (Vioreck and Shandelmeier 1980; Van Cleve and Vioreck 1981; Van Cleve and Vioreck 1983) have concluded that deciduous trees may dominate for the first 100 years on white spruce sites. Our finding that black spruce and deciduous trees co-dominate during the interval between 110-190 years after a fire differs from what other researchers have reported. Foote (1983) found that a codominance of hardwoods and spruce on upland mesic black spruce sites occurs during the interval between 56-90 years after fire. Differences between our data and Foote's could have several causes. Our prolonged co-dominance stage may be due to better deciduous growing conditions on our upland sites versus the sites Foote investigated. Our sites may have been better drained, allowing deciduous trees to sustain themselves longer alongside black spruce. Our sites may have had more seed sources from where deciduous trees could colonize and establish at higher densities. Additionally, the methods used to determine site dominance differed. Previous successional stage investigations used plot measurements across sites of known past burns. This revealed the general density and coverage of all present species, which were then categorized by successional stage based on ages. Our methods used stand reconstructions of dominant overstory tree species to determine the overall pattern of canopy height growth. This method quantified the canopy development from data obtained directly from competing vegetation. This allowed us to determine what species type dominated the canopy for each sampled year.

### ***Mechanisms of Succession***

The majority of stands in the study area appear to be following a SR trajectory rather than SDR. Four of the sixteen paired stands had no significant age difference, which does not conform to the SDR hypothesis. Nine of the sixteen spruce stands were too young to have originated through SDR, and the remaining five spruce stands that were older than 100 years did not contain evidence of senescent deciduous trees. The two stands where SDR occurred as described by our canopy reconstructions comprised less than 15% of the total study area as calculated from visual image classification and field observations.

SR is by far more common than SDR in fire affected sites

Several results support this conclusion about the relative importance of SR versus SDR in the upland boreal forest in Alaska. The typical fire frequency in upland forests in Interior Alaska constrains the possibility that SDR can occur. If a stand burns before spruce has time to assume dominance, SDR cannot occur. Assuming the sampled tree ages can be used as a surrogate for time-since-last-fire, they are consistent with a fire frequency of <100 years. One may argue that human activities have increased fire frequency on Ester Dome, yet the fire frequency of remote watersheds in Interior Alaska suggest a similar <100 year interval (Fastie and Lloyd 2003; Duffy, Rupp, and Mann unpublished data).

While the two models of post-fire vegetation succession in Interior Alaska have been known for some time, the relative importance of each at a landscape scale has not been sufficiently investigated. Our results suggest that over half of our sampled stands across a 47 km<sup>2</sup> area have not resulted from a SDR successional trajectory while the SR trajectory has been the dominant form of post-fire recovery in this area. This is an important result for several reasons. If the SR pathway is followed, a site can return to spruce domination much sooner and thus be more prone to future burning than if SDR was occurring. This may affect efforts of forest managers to reduce fire risk by treating black spruce stands around communities in order to set succession back to a deciduous stage as the SDR hypothesis explains. If these stands are located in areas similar to our study region, such treatments may result in black spruce immediately re-establishing with little decline in fire risk. Additionally, when modeling the interactions of fire, vegetation and climate over long time periods, the successional trajectory followed can dramatically impact future vegetation patterns, fire return intervals, and atmospheric emissions of trace gases (Rupp et al. 2002). Finally, the ability of black spruce ecosystems to store carbon may be a sinusoidal pattern over time, assuming a continual SR pathway. This repetitive pattern of old black spruce stands storing large amounts of carbon, then burning and releasing those carbon stocks, then immediately reestablishing themselves and locking up carbon, would have large impacts on global warming scenarios that rely on carbon modeling dynamics.



## Conclusion

Past research has shown that both SDR and SR successional pathways occur in Interior Alaska, but little is known about their relative importance at landscape scales. In stands undergoing SR after fires, pre-fire dominants immediately reclaim site dominance by root sprouting or by seeds originating from semi-serotinous cones. In stands undergoing SDR, early successional species like aspen and birch are gradually replaced by black and white spruce. These sites must be able to support both deciduous and spruce species and have a sufficiently long fire return interval to allow spruce to gain dominance of the site.

By classifying the major vegetation types and modeling them according to topographic variables of summer insolation and elevation, we were able to accurately predict 51% of all species, and 78% of spruce in the study area. The ability to predict the majority of spruce coverage with spatially determined variables, while ignoring the temporal aspect SDR assumes, leads us to believe that SDR is not the dominant form of succession in the study area.

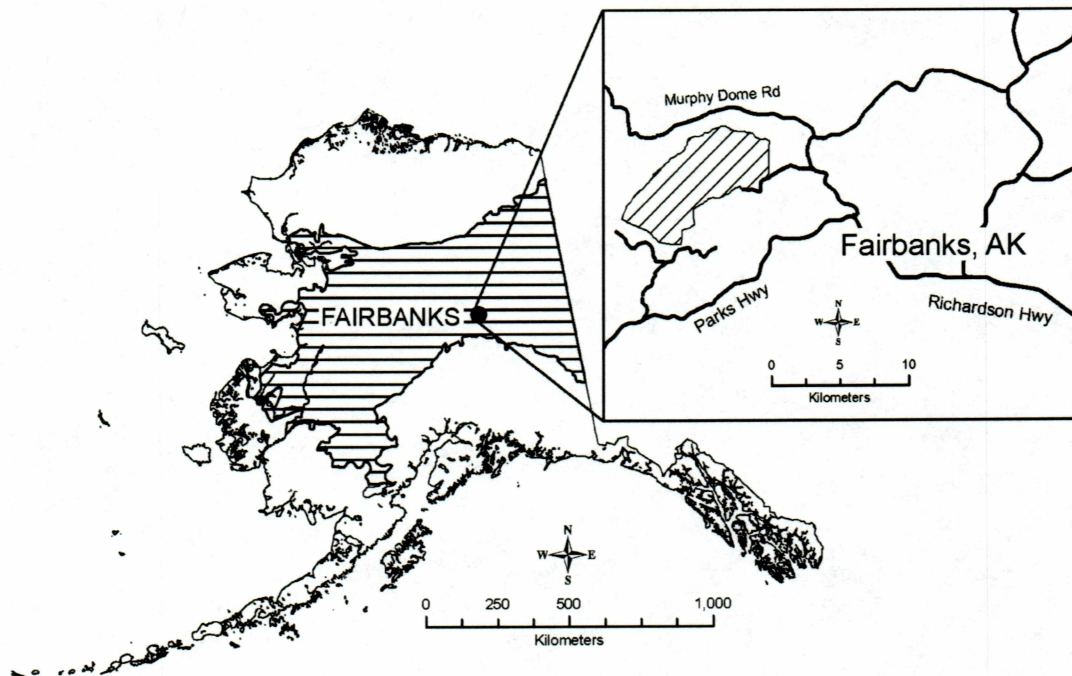
able to predict occurrence just based on topography → this is much different than what I have noticed.

By studying two stands where senescent birch trees co-mingle with dominant black spruce, we estimate that a minimum of 100 years is required for SDR to occur in the study area. Our initial hypothesis, in accordance with the SDR hypothesis, was that the mosaic was the outcome of varying times-since-last-fires. Tree coring revealed this to be

unlikely for most stands. Four pairs of stands had no significant age difference, nine of sixteen spruce stands were too young to have undergone SDR, and none of the spruce stands that were old enough to have originated through SDR contained senescent deciduous trees as mediated by the SDR hypothesis. Through field observations and visual classification, we estimate the two stands where we document SDR comprise at most 15% of the study area.

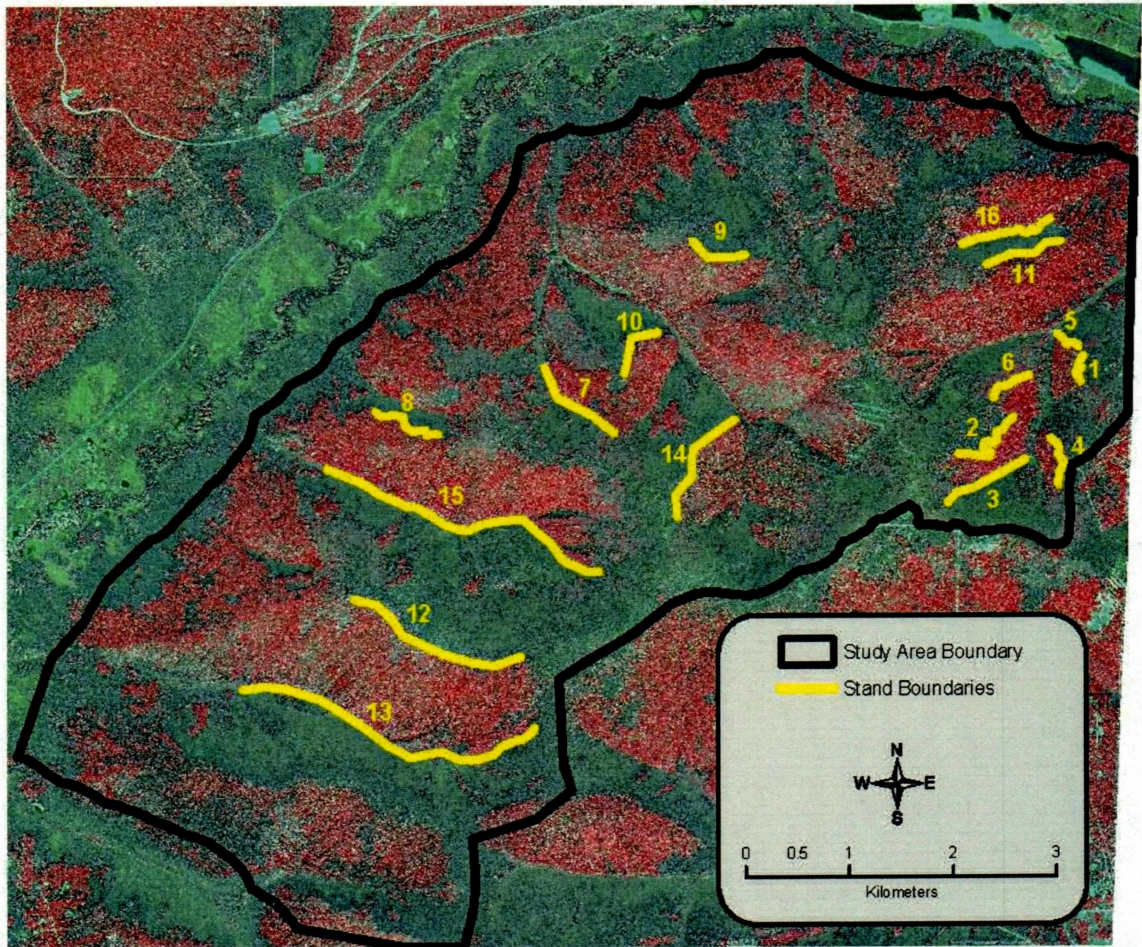
This topographically diverse setting has such extreme environmental growing conditions that only spruce has the ability to dominate many sites. Once spruce gain such expansive dominance, the ability of other species to out-compete them declines. A low <sup>✓ shouldn't it be high?</sup> fire frequency in the study area is most likely limiting SDR from occurring because fire occurs before these possible SDR sites have time to relay dominance to spruce, which leaves SR as the dominant form of succession. ^

Stand ages and compositions are also consistent with SR being the dominant mechanism of secondary succession on Ester Dome. This result is consistent with the fire frequency typical in Interior Alaska. The 70 to 100-year fire frequency typical of upland forests here probably interferes with SDR before it has time to reach completion, leaving SR as the most important mechanism.



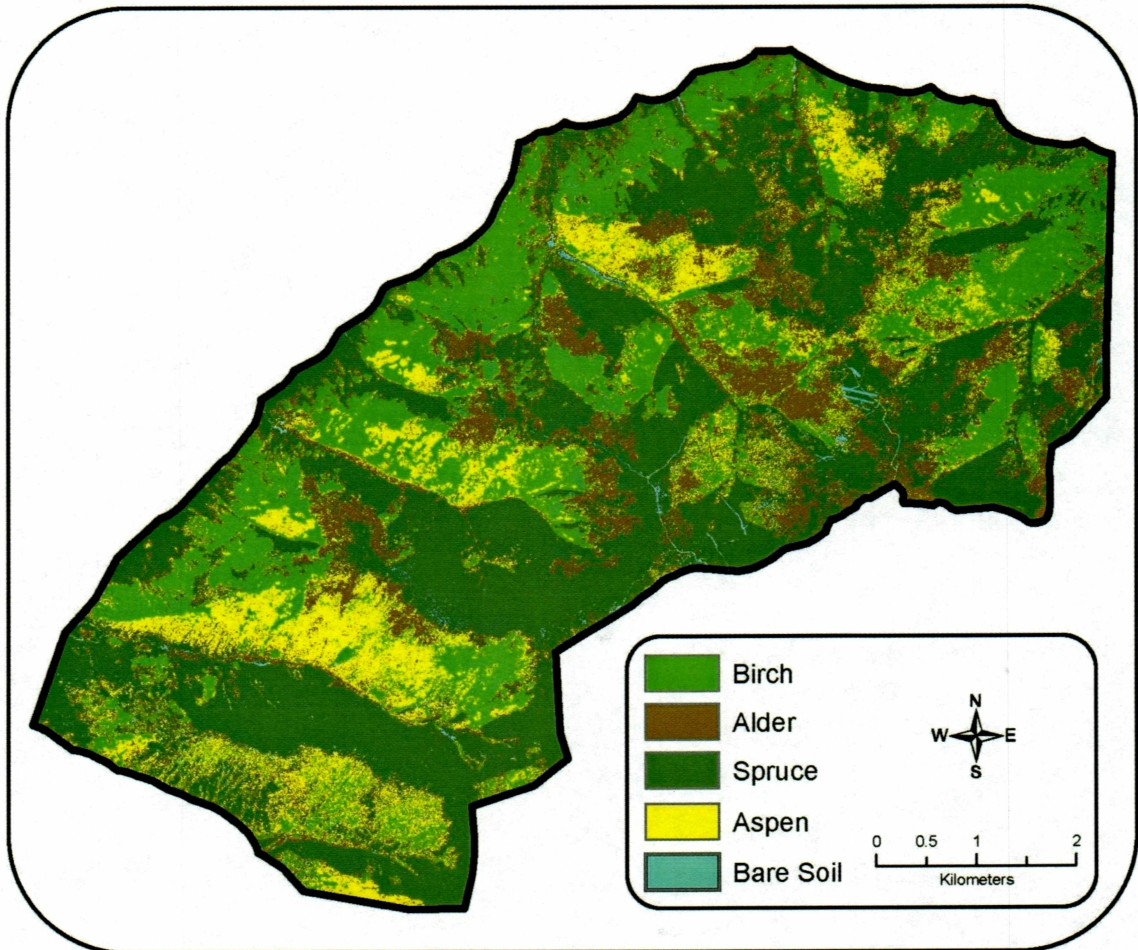
**Figure 1:** Location of Ester Dome study area within Interior Alaska.



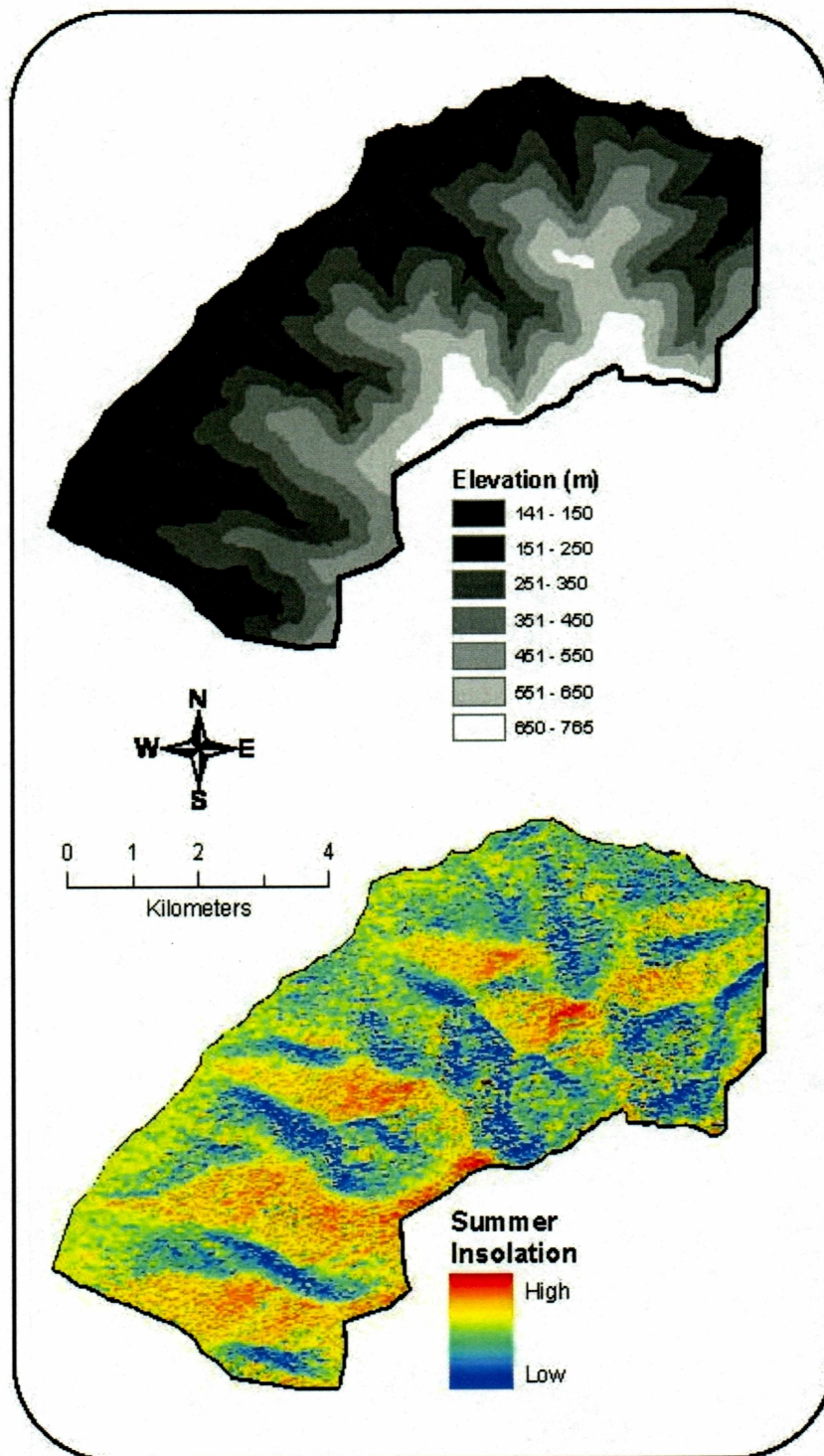


**Figure 2:** Near infrared satellite image showing locations of 16 sampled stand borders distributed across the study area.



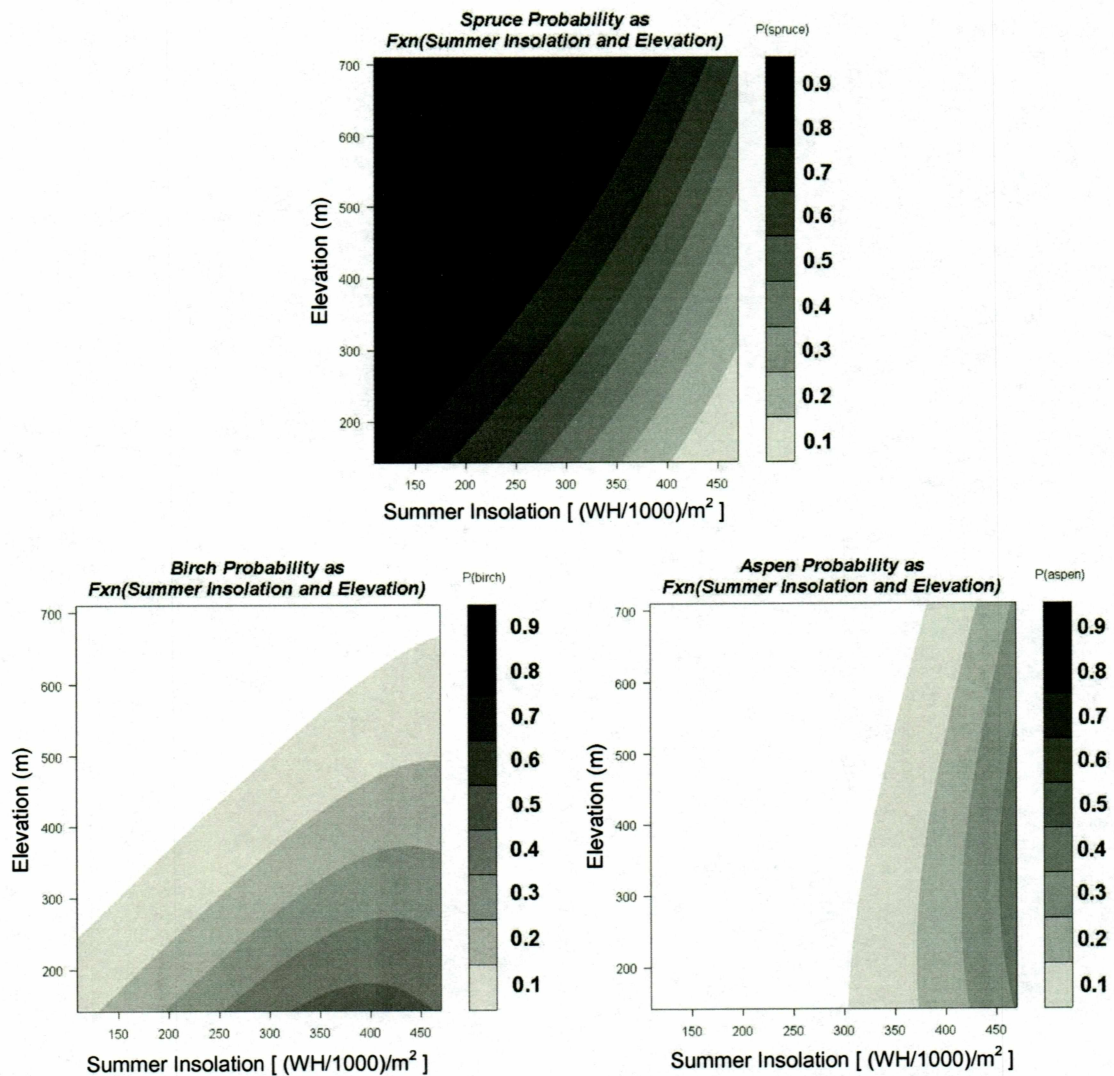


**Figure 3:** Supervised image classification of Ester Dome study area. Vegetation classes are used as response variables with topographic covariates in a multinomial logistic regression model.

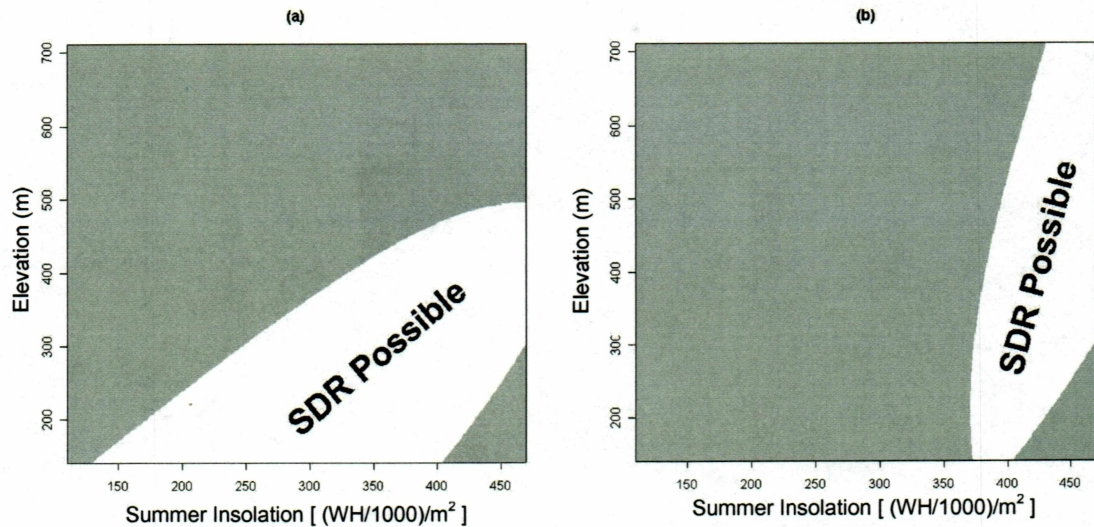


**Figure 4:** Significant model covariates. Elevation and summer insolation were the significant ( $\alpha = 0.05$ ) topographic variables in the final multinomial logistic regression model.

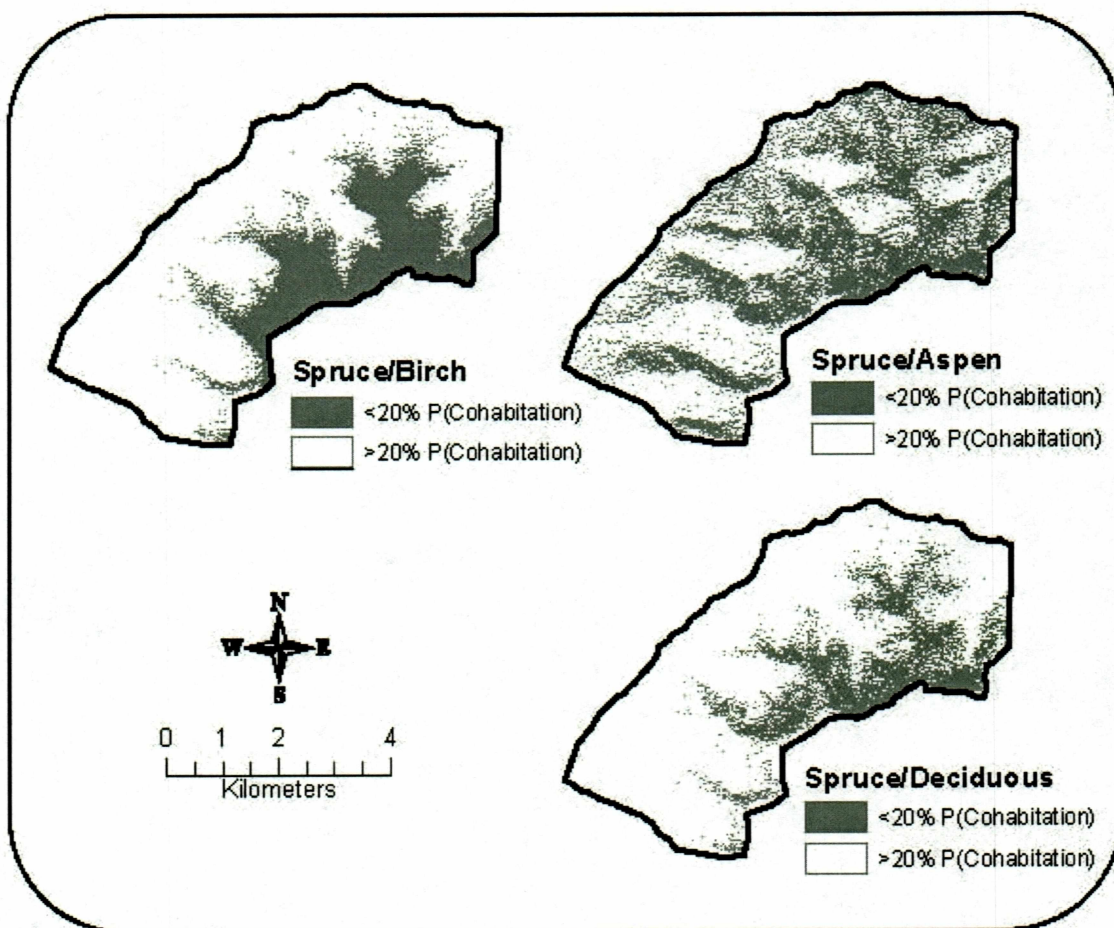




**Figure 5:** Vegetation probabilities of spruce, birch, and aspen classes. These plots were produced by transforming the multinomial logistic regression results into probabilities based on the significant covariates of elevation and summer insolation.

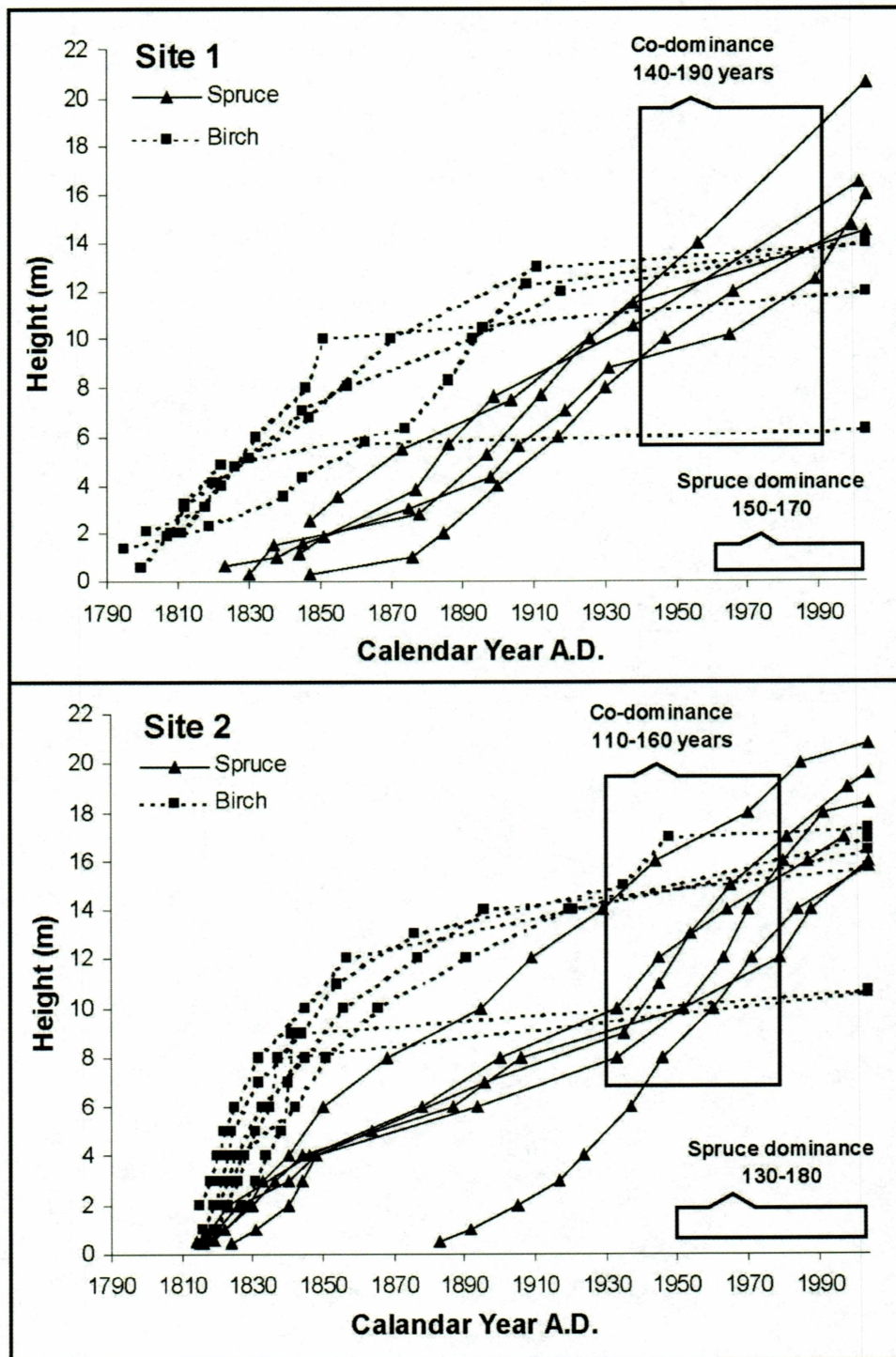


**Figure 6:** SDR regions. Plots were generated by combining the spruce/birch and spruce/aspen plots from Figure 5 for those areas having >20% probability. Unshaded regions have >20% probability of supporting both spruce and birch (a) and spruce and aspen (b) associations, which indicates where SDR is possible. Shaded regions have <20% probability of supporting both spruce and deciduous species.

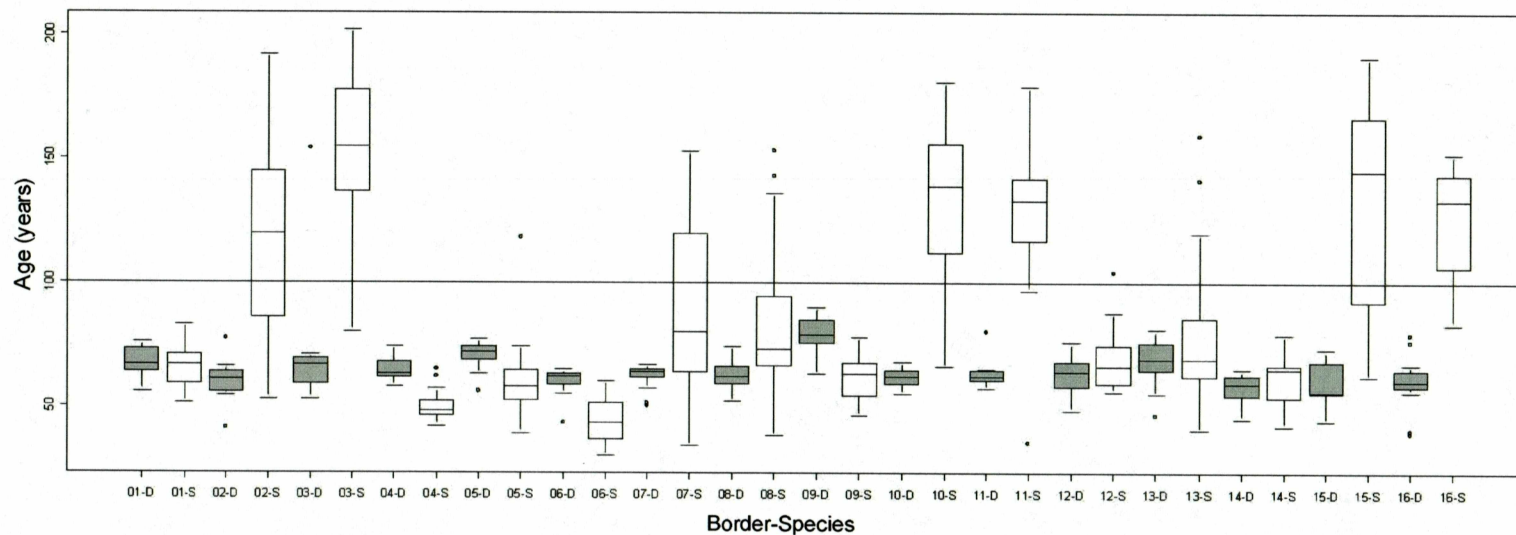


**Figure 7:** SDR regions. Cartographic representation of Figure 6. Unshaded regions have >20% probability of supporting both spruce/birch and spruce/aspen associations, which indicates where SDR is possible. Shaded regions have <20% probability of supporting both spruce and deciduous species.





**Figure 8:** Stand growth reconstructions of two sampled stands. Boxed areas indicate estimated successional stand age requirements for the co-dominance and spruce dominance stages used in testing the SDR hypothesis.



**Figure 9:** Box plots of 16 sampled stand borders (32 individual stands represented by numbers) between deciduous (D, shaded) and spruce (S, unshaded) species. The boxes contain the middle 50% of the data with the sample median represented as a horizontal line within the box. Lines extending from the boxes include over 99% of the data. Suspect outliers are indicated by circles. The continuous horizontal line indicates 100 years of age.





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